ECOLOGICAL ASPECTS OF INDIAN SPINY-TAILED LIZARD
UROMASTYX HARDWICKII IN KUTCH

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Allocation of three major resources – space, food and time by the Indian Spiny-tailed Lizard *Uromastyx hardwickii* (Lacertilia: Agamidae) was studied in the grassland habitat of Kutch. The activity budget, behavioural thermoregulation, foraging behaviour and social interactions were observed using focal animal sampling combined with scan animal sampling and *ad libitum* sampling. Seasonal food habits were estimated from bite counts and pellet analysis. Ranging patterns were studied by mapping individually identified lizards. The activity pattern shifted from bimodality in summer (duration=119 min/day, SE=12, n=25 lizards) to unimodality in monsoon (duration=93 min/day, SE=5, n=23 lizards). The body pigmentation changed from dark to light as the temperature increased. The diet comprising grasses (*Chrysopogon* and *Cymbopogon*), insects (ants, termites and locusts) and shrubs (*Clerodendron*) in summer, narrowed to herbs (*Borreria, Euphorbia, Indigofera*, etc.) and grasses (*Chrysopogon* and *Cymbopogon*) in the monsoon. The density of active burrows was 42.45/ha in summer and 66.04/ha in monsoon. The average home range was 0.2 ha (SE=0.04, n=23) in summer and 0.05 ha (SE =0.01, n=20 lizards) in the monsoon. Male home ranges (0.39 ha in summer, SE=0.08, n=6 and 0.12 ha in monsoon, SE=0.03, n=4) were larger than those of females (0.15 ha in summer, SE=0.04, n=4 and 0.03 ha in monsoon, SE=0.02, n=3) and juveniles (0.12 ha in summer, SE=0.02, n=10 & 0.03 ha in monsoon, SE=0.01, n=7). Aggressive behaviours with low overlaps in core areas and extensive overlapping in fringe areas of individual home ranges indicated territoriality in core areas, but hierarchically or temporally spaced resource sharing in the peripheries of home ranges.

Key words: Spiny-tailed Lizard, *Uromastyx hardwickii*, behaviour, activity budget, thermoregulation, food habits, home range, mating structure, density

INTRODUCTION

The foraging behaviour of lizards is correlated with their size, morphology, ecology, reproduction, metabolism and movements, and these relations are more prominent in the case of herbivory, suggesting an evolutionary relationship among these parameters (Vitt and Congdon 1978; Huey and Pianka 1981; Pietruszka 1986; King 1996; Perry and Pianka 1997; Pianka *et al.* 1998). Plants put forward an array of defences against being foraged, constraining an herbivore's diet by toxin intake, limited nutrient intake, slow digestion rates, gut fill and in the case of ectothermic herbivores, daily feeding time (Stephens and Krebs 1986). Thus, a pure plant diet favours specialisations compared to a carnivorous diet. Out of 3,300 species of modern lizards existing today (Sokol 1971; Pough *et al.* 1989; King 1996) only 90, including the Spiny-tailed lizards, *Uromastyx* spp. have an herbivorous diet (King 1996).

Recent phylogenetic studies on *Uromastyx*, previously considered as agamids, showed that they could potentially be classified into a new family, the Uromastycidae (Böhme 1982; Moody 1980; Borsuk-Bialynicka and Moody 1984; Das 2002; but see Joger 1991). Indian Spiny-tailed lizard *Uromastyx hardwickii* (Gray), one of the fifteen under genus

Uromastyx, is a dweller of arid, open and scrubby regions (Das 2002) and has a patchy distribution from north-western India to Pakistan and Afghanistan (Khan and Mahmood 2004). It forages mainly on grasses, shrub leaves, flowers and fruits, and obtains water from food and metabolism of subcutaneous fat (Daniel 2002; Khan and Mahmood 2004). The activity of *Uromastyx* is retarded in winter and intensified in spring and summer, with mating occurring in March or April. The female lays around 14 eggs between April and May-June (Daniel 2002; Das 2002; Khan and Mahmood 2004). Typical populations of this solitary burrow dweller occur in loose associations of several individuals ranging from 10 to 100 per sq. km, often with nearly 50 adults in a colony (Bhatnagar *et al.* 1973; Das 2002; Knapp 2004). They are known to occupy extensive territories (Zug 1993), but details on the nature of their territoriality is lacking.

The spatial distribution of animals is determined by resource dispersion and sociality (Johnson *et al.* 2002). The home range parameters and dynamics reveal various aspects of behavioural ecology (Ferner 1974; Gans and Pough 1982). The territory, the defended and exclusively used part of the home range, may include it in its entirety or some ecologically significant sites or routes (Burt 1943; Schoener 1968; Stamps 1977; Smith 1985). In lizards, the spacing system varies from

clear territoriality to broadly overlapping home ranges (Rose 1982; Smith 1985).

'Vulnerable' (as declared by the IUCN) Indian Spiny-tailed Lizard populations, surviving under the threats of changing land use and trade for supposed aphrodisiac properties, have not been subjected to any detailed ecological study. In this study we evaluate the temporal activity pattern, ranging patterns, social interactions, food and foraging behaviour of the species.

STUDY AREA

The study was conducted in a typical Spiny-tailed lizard habitat in Abdasa taluka, the south-western province of Kutch district, in the state of Gujarat in western India. Kutch is mostly occupied by Jurassic rocks, bears traces of the ancient Indus Valley civilization and partially detached from the mainland owing to the condition of the Rann (Williams 1958). It belongs to the semi-desert ecological zone where summer commences in March and continues until late June. May experiences the highest air temperatures of 40-45 °C. Precipitation is scanty and stochastic, with an annual average of 384 mm. The rains arrive by early July in 65% of the years while late onset is recorded in 35%. A high evapo-transpiration rate results in drying up of most natural water sources. Winters are relatively severe, extending from middle of November to February. The minimum temperatures are recorded in January, with an average temperature of 5 °C. The vegetation in this area has been classified as Northern Tropical Thorn Forest (6B) and sub-classified as Desert Thorn Forest (6B/C1) as per the classification of forest types by Champion and Seth (1968). This area, lying in Biogeographic Zone 3B (Kachchh Desert) (Rodgers *et al.* 2002), serves as the habitat of several important species of fauna, some of which have been declared as Schedule I under the Wildlife (Protection) Act, 1972 (Home 2005).

METHODOLOGY

An area of 2.1 ha was selected and delineated in Kanauthia Daun (23°14' N; 68°59'E), a grassland habitat with a good population of Spiny-tailed Lizards. Infrequent patches of shrub enhance the visibility in this part. The intensive study area, with details of the vegetation was mapped using a compass, range finder and hand-held GPS unit (Garmin 12 XLS).

Individual lizards were identified from visual clues: size, sex (males have a longer, larger tail with a bulbous base) and natural marks (stripes and blotches in young, body notches, broken tails, missing spines and scales, sloughed skin etc.). Identified lizards were continuously followed one

at a time for the first two weeks to locate their burrows which were mapped, and a detailed catalogue was prepared. Since adult, sub-adult and juvenile lizards used a single burrow each, a total count of lizards was done once in each season for density and age structure estimations and nearest neighbour analysis was performed for the pattern of burrow distribution. The average distance of hatchling burrows from adult burrows was tested with that from equal number of any burrow (all selected randomly) through a 't' test to find any spatial affinity between adults and their hatchlings. Morphometric data were obtained whenever lizards were rescued from poachers.

Observations were done from a hide with 8×50 binoculars in summer and monsoon, and data were recorded after an initial period of habituation for two weeks. Scan animal sampling (Altmann 1973) at 10 minutes intervals was used to record the activity pattern from 0800 to 1730 hrs in summer and 0900 to 1830 hrs in the monsoon. The activity was categorised into six discrete states: scanning, basking, moving, foraging, social interactions and escape. Activity pattern was quantified as number of active lizards at any time expressed as percentage of the maximum lizard count for the day.

Identifiable individuals' locations were recorded on the map of the study site for each scan using a compass and range finder with reference to mapped features of the study area. The home range size was estimated from these locations using a 95% fixed kernel contour (Worton 1989) and the core area was delineated from a 50% isopleth. The percent overlap between a pair of neighbouring lizard home ranges was computed. *Ad libitum* sampling was done for territorial and other social behaviours. Territorial behaviour was classified as only chase (low intensity), displays (medium intensity) and aggressive fights (high intensity). Occurrences of aggressive behaviour were expressed as aggression-encounter rates (AER= frequency of occurrence of aggressive behaviour/ sampling day/ha).

Ambient and ground temperatures were recorded at every half hour intervals using a Hick's air thermometer. Corresponding to each temperature record, the numbers of active juvenile, sub-adult, adult female and adult male lizards were recorded. The average lizard sighting (activity rate) was calculated for each temperature class. The body colours of individuals within 30 m were categorised into dark brown, dark olive, light olive, yellow and pale white and analysed for any pigmentation trend in relation to ambient and ground temperatures. Bite counts of lizards in proximity to the hide (<30 m) were recorded by focal sampling of individual lizards between subsequent scans. On the average, a scan took 2 minutes, and an interim 8 minutes were used for focal sampling of foraging lizards. The area sampled for bite counts was about 13% of the study area and had a similar vegetation

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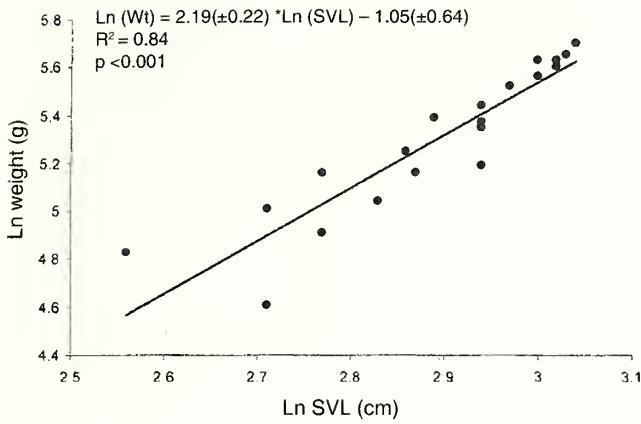J. Bombay Nat. Hist. Soc., 104 (3), Sep-Dec 2007

Fig. 1: Relationship between log-transformed snout-vent length
(SVL) and weight of *Uromastyx hardwickii*

composition. Data were recorded as the number of bites of different food items using a tally counter. An actively foraging, focal lizard was observed till >20 to <200 bites were recorded or it moved away from the 30 m radius or stopped foraging. The dietary composition was also studied through faecal pellet analysis (Korschgen 1980). Three random transects of 100 m x 2 m were sampled for pellets. Pellets were collected on every alternate day, weighed accurately and transferred into Zip locks for later analysis. However, pellet collection was poor in the monsoon due to the faster decomposition rate, and this method was not used for diet analysis in the monsoon. Simpson's index of diversity, B= 1/$\sum$ pi2 (Mac Arthur 1972) where pi indicates the ith food item, was used to quantify the trophic niche breadth. The dietary preference was estimated through compositional analysis (Aebischer *et al*. 1993). The vegetation was sampled by hand plucking all available bites of each food species from randomly selected 1 m x 1 m quadrates for grasses and herbs and 4 m x 4 m quadrats for shrubs to quantify the forage availability. Bites were simulated by hand plucking of plant parts, which were oven dried in paper bags at 70 °C to obtain the dry weights (Harris 1970; Wallamo *et al*. 1973; Jhala 1997). The daily forage intake (dry weight) was estimated from the number of bites taken by the focal lizard per day.

SIMSTAT Version 2.5 (Provalis Research 1995), SPSS Version 8.0 (SPSS 1997) statistical software and Arc View Version 3.2 and Arc View extensions (Animal Movement SA v 2.04 beta and Image Support, Geoprocessing and Spatial Analyst) (L30) GIS software (ESRI 1999) were used for analysis.

RESULTS

A significant linear relationship was obtained between log-transformed snout vent length and weight from 22 lizards

(Fig. 1). The ratio of snout-vent lengths between male and female lizards was 1.09.

Density, spatial distribution and structure of burrow; population age structure

Spiny-tailed Lizards resided solitarily in burrows. Hatchlings resided with their mother during the initial days. Occasionally, they emerged from their mothers' burrows, foraged for short spans and returned swiftly; such explorations took place under the vigil of the mother. The density of burrows increased from 42.45/ha in summer to 66.04/ha in the monsoon, mainly due to new recruitment. The diameter of burrows was a good surrogate in determining the age of lizards residing in them (Fig. 2). Seasonal fluctuations were found in the age structure of the population (Fig. 3).
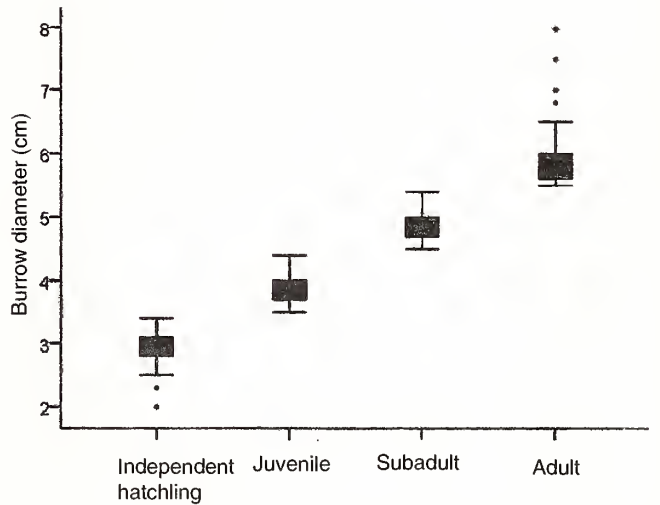

Fig. 2: Box plot of burrow diameters of various age categories
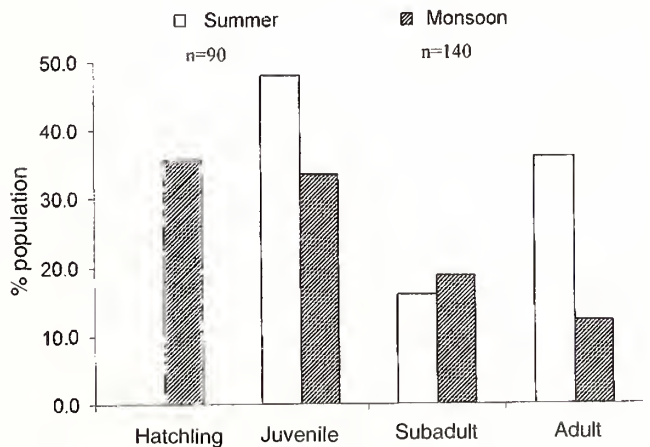of *Uromastyx hardwickii*

Fig. 3: Population structure of *Uromastyx hardwickii* in the
study area as determined from burrow structures

An average, adult burrow, 1.2 m long (SE= 0.05, n=10), 0.5 meters deep (SE= 0.04) and 6.6 cm in diameter (SE= 0.3) comprised of three distinguishable segments. The tunnel ran straight down for about 0.7 m (SE =0.06) at an angle of 27° (SE =1.1) with the surface. Then it went down steeply for 0.5 m (SE= 0.05, n=6) at an angle of 28° (SE= 1.7). Sixty per cent of the burrows showed a change in trajectory between the two segments. The tunnel ended in a horizontal, box shaped chamber of size 17 cm (SE =1.8, n=7) (Fig. 4).

The spatial distribution of burrows analysed through nearest neighbour analysis (Rossbacher 1986) showed a clumping tendency (hatchlings: $|Z|$=13.27, r=0.019; juveniles: $|Z|$=12.87, r=0.018; sub adults: $|Z|$=9.62, r=0.14; adults: $|Z|$=7.57, r=0.011) (Fig. 5). But, there was no spatial affinity between adult and hatchling burrows (one tailed 't' test: t=0.20, p=0.42).

Time budget and activity pattern of Spiny-tailed lizards

The Spiny-tailed lizards were strictly diurnal. Minimum activity was noticed during winter. The daily activities followed the following sequence. Emerging animals scanned their surroundings for conspecifics and predators; initially they basked flat near the burrow and later basked high on grass tussock. Gradually, they became fully active, moved, foraged and interacted. Group escape was a common anti-predatory behaviour. Re-emergence occurred only after the departure of the predator(s).

The maximum density of active lizards for a day was estimated to be 34/ha (SE =1.38, n=20 days) in summer and 28/ha (SE =4.44, n=20 days) in the monsoon. The animals remained active for 119 minutes (SE =12.13, n=25 lizards) or 8.3% of the day during summer and 93 minutes (SE =4.94, n=23 lizards) or 6.5% of the day during monsoon with basking constituting 16% (in summer, SE =1.42, n=25 lizards) and 37% (in monsoon, SE =1.6, n=23 lizards) of the daily activity duration and foraging constituting 55% (in summer, SE =2.7,
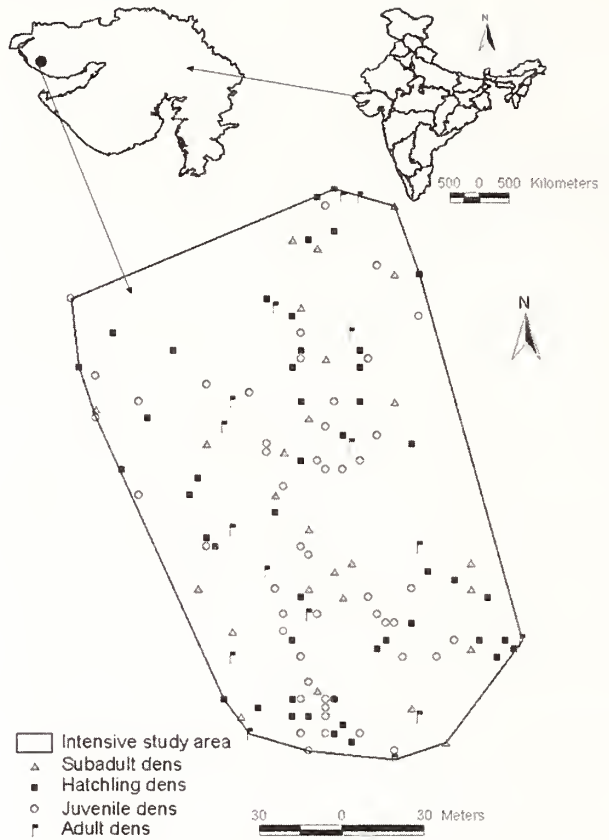

Fig. 5: Map of intensive study area showing the spatial distribution of *Uromastyx hardwickii* burrows along with geographical location of the study site

n=25 lizards) and 41% (in monsoon, SE =2.0, n=23 lizards) of the daily activity duration (Fig. 6). There was no difference in activity duration between seasons (Mann Whitney U test; $|Z|$=0.26, p=0.80).

The activity pattern was bimodal in summer. Activity showed a major peak between 0900-1100 hrs and a minor peak around 1500 hrs. As the summer progressed, the major peak increased in height and the minor peak declined, although duration of activity remained unaltered. Bimodality changed to unimodality during the monsoon with the peak of activity between 1200-1500 hrs. In monsoon, activity pattern was highly unpredictable due to overcast skies (Fig. 7).

Temperature, activity and behavioural thermoregulation

The ground temperature ranged between 30 °C and 52 °C in summer and between 29 °C and 45 °C in the monsoon. The optimum near ground temperature for activity was 39 °C-41 °C. Larger lizards tended to be active within a narrow temperature range compared to smaller lizards (Fig. 8).

There was gradual and sequential replacement of body colours across the gradient of ambient and ground
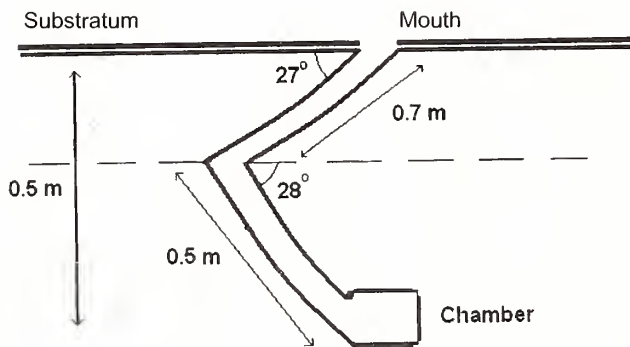

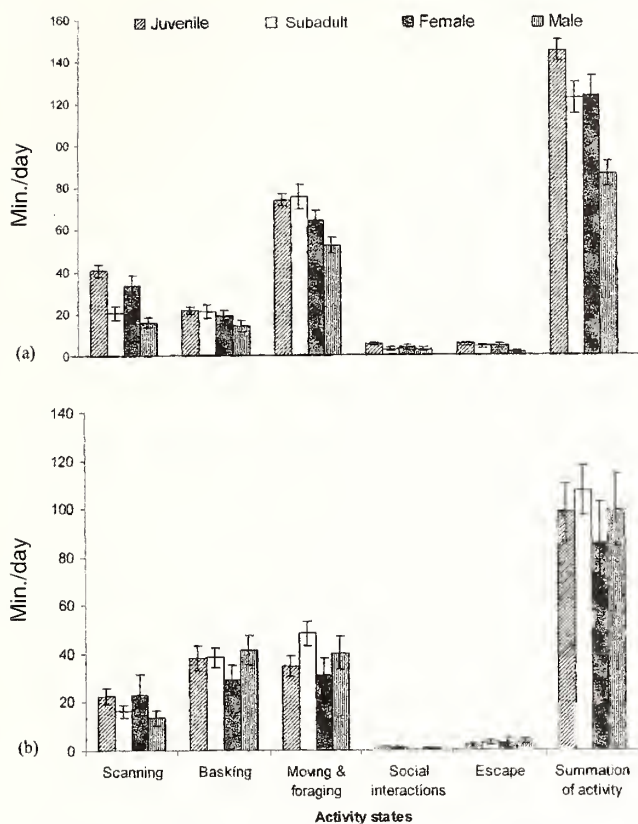Fig. 4: Diagrammatic representation of a typical *Uromastyx hardwickii* burrow

Fig. 6: Activity budget of various size classes of *Uromastyx hardwickii* during (a) summer, (b) monsoon.
(Error bars are standard errors)

Fig. 7: Seasonal comparison of temporal patterns of active
Uromastyx hardwickii
(Error bars are 95% confidence intervals)

appeared much darker than in summer and retained a dark brown coloration throughout the day.

Movements and territoriality

The average estimated range size of the lizards in summer (2,332 sq. m, SE=384, n=23) was larger (t=4.59, p<0.001) than the average range in the monsoon (545 sq. m, SE=111, n=20). An average male home range was more than twice that of a female whereas the home range of adults and sub-adults was twice that of juveniles (Fig. 10). Home ranges showed extensive overlaps. The average overlap between adjacent ranges was 23% (SE =1.35, n=23) in summer and 11% (SE =3.65, n=20) in the monsoon, but the core area overlap was only 4.5% (SE =0.54, n=23) in summer and 0.5% (SE =0.29, n=20) in the monsoon. Overlaps were similar between the ranges of different ages and genders (χ^2=7.027, DF= 8, p= 0.534), but the extent of overlap varied seasonally

temperatures in summer, with darker pigments appearing at lower temperatures and lighter pigments at higher temperatures. Another behavioural feature associated with lighter pigmentations was arching of the tail to reduce body contact with ground (Fig. 9). During monsoons, the lizards
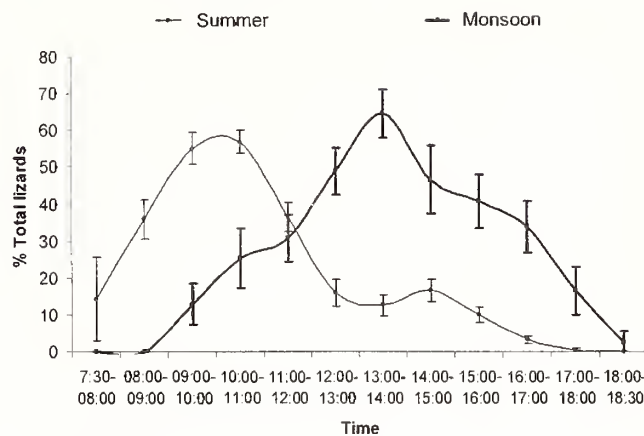
Table 1: Average percentage of home range overlaps among different size classes of *Uromastyx hardwickii*

		% Home range	
		Juvenile & subadult	Adult female	Adult male
		Area 95% fixed kernel		
Overlapped by	Juvenile and subadult	22 (5.7)	21 (6.0)	10 (5.3)
	Adult female	25 (1.9)	15 (11.8)	17 (12.9)
	Adult male	29 (5.9)	38 (18.8)	33 (8.8)
		Core 50% fixed kernel		
	Juvenile and subadult	5.4 (1.4)	1.6 (1.1)	3.3 (0.9)
	Adult female	2.6 (0.7)	0.6 (0.4)	3.1 (1.3)
	Adult male	7.5 (1.7)	8.4 (3.4)	7.3 (1.8)

Value in each cell represents the average percentage range area of the age-gender class in column, overlapped by the age-gender class in row. Standard Errors given in parentheses
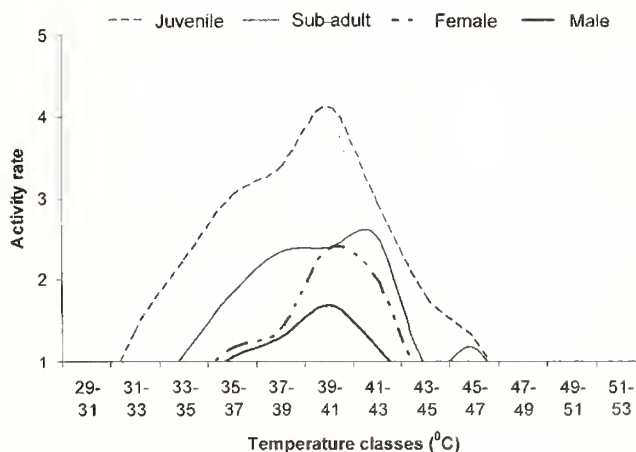

Fig. 8: Ground temperature preferences for activity of *Uromastyx hardwickii* determined as average lizard sightings at different temperatures

Table 2: Aggression encounter rates among different size classes of *Uromastyx hardwickii*

	Intensity	Adult male	Adult female	Juvenile and subadult	Hatchling
Adult male	Chase and display	0.3	0.1	0.1	0.0
	Fight	0.5	0.0	0.0	0.0
Adult female	Chase and display	0.1	0.5	1.9	0.0
	Fight	0.0	0.1	0.2	0.0
Juvenile and subadult	Chase and display	0.1	1.9	2.6	0.9
	Fight	0.0	0.2	1.0	0.0
Independent Hatchling	Chase and display	0.0	0.0	0.9	0.6
	fight	0.0	0.0	0.0	0.4

Frequency of occurrence of aggressive behaviour (chase and display or fight/sampling day/hectare) given in cells for each pair of age-gender classes

(ANOVA; F= 36.17, p= 0.009) (Table 1). Detailed analysis of five female home ranges showed that although an average male overlapped >20% to <40% of three female ranges (SE= 0.7) and >60% to <80% of only one female range (SE =0.6), there was high degree of variation among individual males (Fig. 11).

The lizards were much more aggressive during summer. Fights were common in the core areas and chases and displays were common, in the peripheries of home ranges (Fig. 12). The correlation between the extent of home range overlap
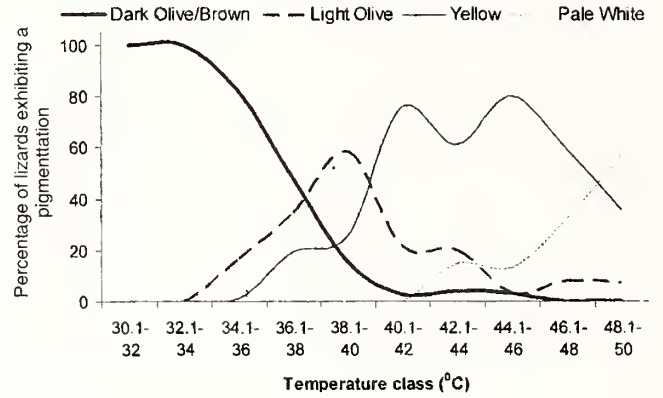
Fig. 9: Percentage of *Uromastyx hardwickii* showing various pigmentations at different ground temperatures during summer

and rate of aggressive encounters was insignificant (r=0.005, p=0.99). The maximum territorial aggressions were observed between juveniles and sub-adults followed by females and juveniles, mostly in the form of chase and displays. Males showed tolerance towards other classes and infrequent aggressions among each other, which mostly took the form of severe fights. Even independent hatchlings were aggressive towards each other (Table 2).

Foraging behaviour of Spiny-tailed lizards

The results obtained from bite count and faecal pellet analyses were similar. Spiny-tailed lizards were 'active foragers'. During summer, foraging was mainly restricted to morning. From bite counts, the lizard diet was found to have

Table 3: Seasonal food habits of *Uromastyx hardwickii* and seasonal food availability (no. of bites available/sq. m)

|	Utilisation				Availability			
	Summer		Monsoon		Summer		Monsoon	
Food items	% bites	S.E.	% bites	S.E.	% bites	S.E.	% bites	S.E.
Chrysopogon	36.2	2.0	18.8	4.2	40.2	11.8	8.0	3.6
Cymbopogon	47.0	2.3	17.8	4.2	44.6	11.6	7.0	2.0
Aristida	0.0	0.0	2.0	0.7	0.0	0.0	1.6	1.2
Alternanthera	0.0	0.0	19.4	3.4	0.0	0.0	14.2	4.0
Anisomeles	0.0	0.0	7.3	1.6	0.0	0.0	5.0	2.3
Borreria	0.0	0.0	9.9	1.3	0.0	0.0	29.3	6.7
Euphorbia	0.0	0.0	6.6	1.6	0.0	0.0	6.3	1.9
Indigofera	0.0	0.0	8.6	1.6	0.0	0.0	7.5	2.6
Other herbs	0.0	0.0	1.4	0.5	0.0	0.0	20.7	6.7
Vernonia	0.0	0.0	2.6	1.6	0.0	0.0	0.6	0.6
Grewia	0.0	0.0	4.6	4.2	0.0	0.0	0.6	0.6
Clerodendron	6.5	1.2	0.0	0.0	6.9	6.9	0.7	0.7
Insects	10.3	2.1	0.8	0.5				
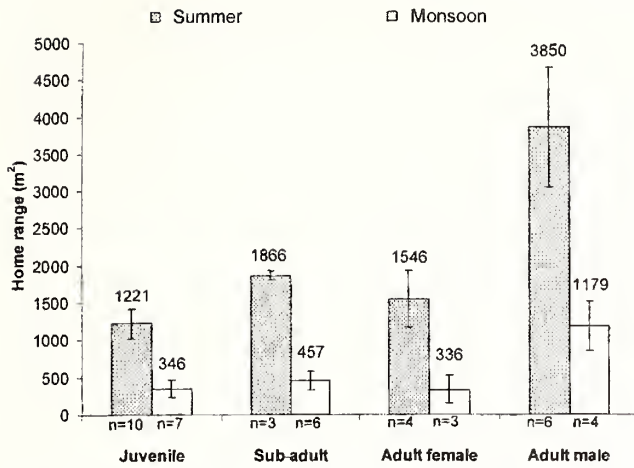
Fig. 10: Seasonal and intra-specific variations in home range
size of *Uromastyx hardwickii*
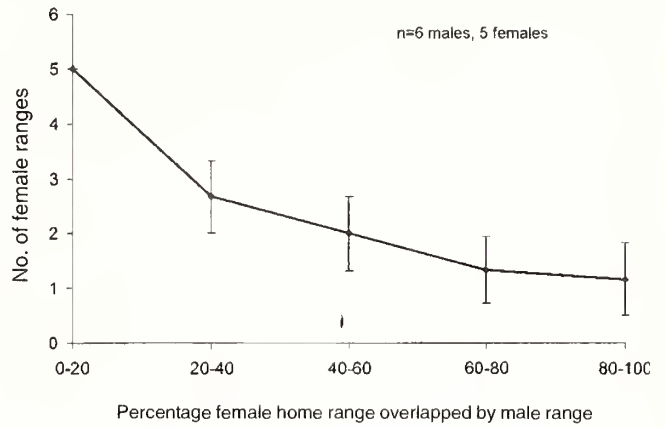(Error bars are standard errors)

Fig. 11: Number of female ranges overlapped to various
extents by an average male range
(Error bars are standard errors)

grasses such as *Chrysopogon fulvus* and *Cymbopogon distans* (78% occurrence, SE =3.1, n=1892 bites), insects such as ants, termites and locusts (10% occurrence, SE =2.01), shrubs (6% occurrence, SE =1.16) and non-food items such as stones and sloughed skin. Food use was proportional to availability. The standardized niche breadth was 0.6.

In the monsoon, foraging took place throughout the day. Herbs (56% occurrence, SE=5.32, n=3486 bites) and grasses (40% occurrence, SE=8.03) constituted the major part of the diet. Shrubs (4% occurrence, SE =2.65) and insects (<1% occurrence, SE =0.48) were consumed less. Food use was not proportional to availability (χ^2=55.89, DF=10, p<0.0001). The scale of preference revealed by compositional analysis was:

Alternanthera > Cymbopogon > Indigofera > Anisomeles > Chrysopogon > Borreria > Euphorbia > Aristida > Vernonia > Grewia > other herbs (Table 3).

Herbs contributed 73% of the dry weight while grasses contributed only 24% and shrubs even less to the diet of the

lizards in monsoon (Table 4). The forage intake (dry weight) was 4.1 gm / day (SE =0.4, n=16 days). Standardized niche breadth was 0.5. Proportion of the food items in the diet stabilized after 80 pellets were analysed (Fig. 13). The food availability varied greatly between seasons.

DISCUSSION

The survival strategies under conditions of extreme temperatures and low food availability revealed from this study hinted at the underlying 'trade-offs' that had to be made during the evolution of the species.

Excluding the quarter-year winter hibernation, the lizards could utilise barely two hours a day for daily activities as the flow was interrupted by frequent livestock grazing, predators and extreme thermal conditions. Associated with each activity were certain costs in terms of predation risk, overheating and/or energy expenditure and benefits in terms of energy gain and/or mating success. Coping with the time

Table 4: Biomass consumption of various food items by *Uromastyx hardwickii* during monsoon in Kutch

Food items	Bite counts	Percentage of bites in diet	Fresh weight/bite	Dry weight/bite	Dry weight in 100 bites	Per cent dry weight in diet
Chrysopogon	37	16.97	0.084	0.018	1.80	16.19
Cymbopogon	46	21.10	0.084	0.010	1.00	8.99
Anisomeles	14	6.42	0.100	0.023	2.33	20.98
Alternanthera	42	19.27	0.116	0.013	1.33	11.99
Borreria	22	10.09	0.103	0.015	1.50	13.49
Euphorbia	19	8.72	0.072	0.016	1.56	13.99
Indigofera	21	9.63	0.090	0.016	1.60	14.39
Others	17	7.80	—	—	—	—

Dry weights of simulated plant parts and percentage bites of each were used to obtain the percentage dry weight of each food item in the diet

Low intensity aggression — Active individuals in close proximity chased one another over short distances along a curve.

One individual retreated on being chased.

Medium intensity aggression — No immediate retreat; confrontation led to display behaviour characterised by dorso-ventral compression with lateral inflation of the body and fast ad press movements.

Display fetched results, brought an end to territorial behaviour; one individual retreated.

High intensity aggression — No significant results of display behaviour; aggressive fights took place characterised by face-off postures, moving and jumping in circles, chasing and biting each other. One individual submitted and the dominant individual mounted on it.
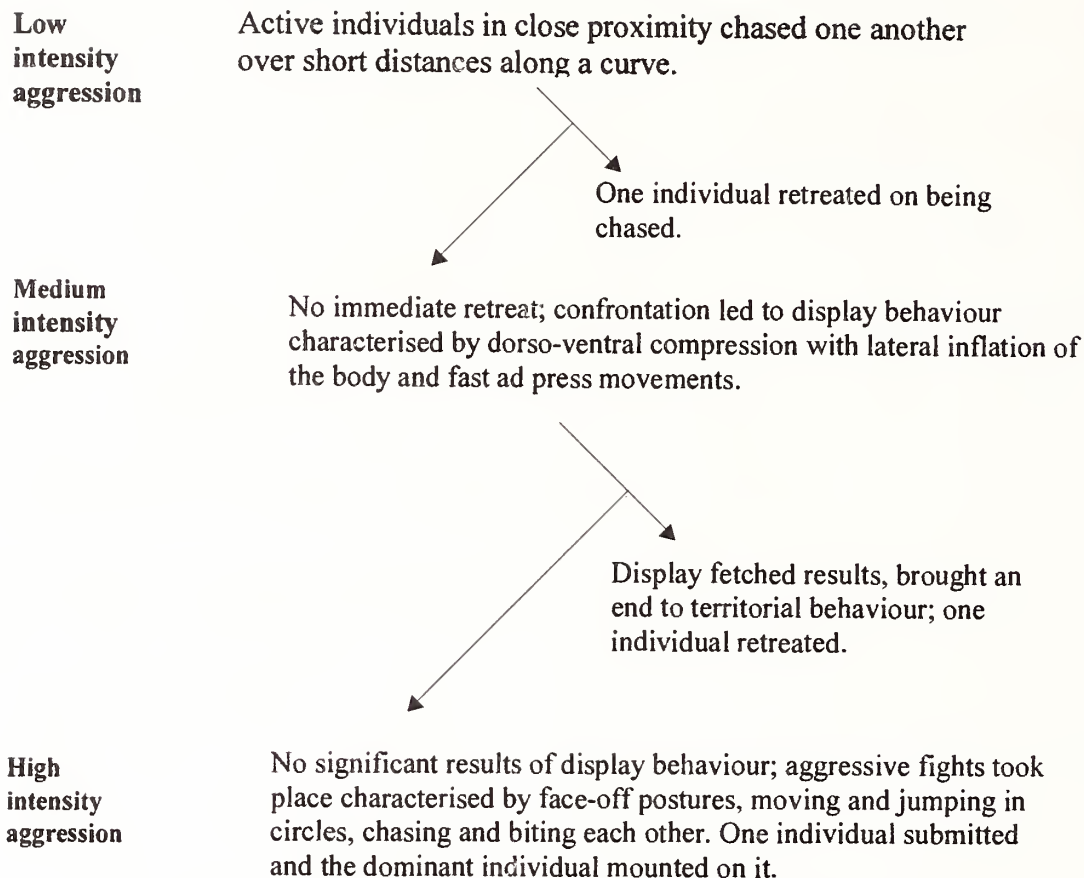
Fig. 12: Sequential pattern of territorial aggression in *Uromastyx hardwickii*

constraint, involved time budgeting with trade-offs. The relative proportions of activities in the behavioural repertoire represented the evolutionarily optimised time allocation to maximize the net benefit and thereby, fitness. The metabolic rate per se (Bartholomew and Tucker 1964) would determine, among other things, the activity duration and foraging
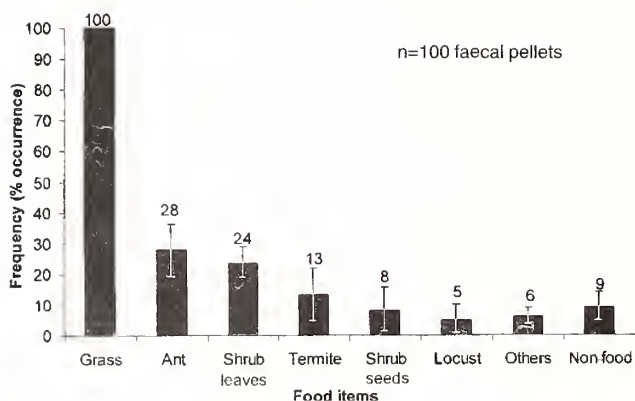

Fig. 13: Food habits of *Uromastyx hardwickii* during summer expressed as frequency of occurrence (percentage) of various food types from pellet analysis
(Error bars are bootstrap 95% confidence intervals)

behaviour of a species. Earlier studies associated a lower per body weight metabolic rate of large agamids (>300 gm) with a nutrition poor, herbivorous diet (Pough 1973) and reduced activity had always been a rule among herbivorous lizards (Andrews 1971; Iverson 1982); the probable reasons being a quick gut fill (Auffenberg 1979; Auth 1980), prolonged food passage time (Harlow *et al.* 1976; Iverson 1982) and temperature-dependent digestibility (Harlow *et al.* 1976; King 1996). A similar trend was observed in the congeneric *Uromastyx phylbi* (Zari 1996). The burrow mouths were kept open for a considerable time in the early morning, stimulating the animal to emerge, and blocked with loose soil on retreat. This maintained a thermal refuge for the lizards under temperature extremes and protected them from predators. Another anti-predatory strategy was the occasional bend seen in the burrows, probably in response to the burrow digging habit of some carnivores such as *Canis aureus*, *Vulpes bengalensis* and *Mellivora capensis*.

The combination of scarce resources and a severe environment provided minimal space to specialise. Consequently, the thermal niche use was generalised, naturally asking for thermoregulatory adaptation(s) in this

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thermophilous ectotherm. Intermediate rests, reduced body contact during the hottest hours and efficient use of body pigmentation were the likely behavioural changes. Thermoregulatory use of pigmentation was also reported from *Moloch horridus* (Pianka *et al.* 1998). The relative rates of absorption and radiation vary with the pigmentation gradient, causing desert species to evolve a higher skin reflectivity (Hutchinson and Larimer 1960; Avery 1979). Smaller lizards had to utilize a larger temperature range for activity as the foraging efficiency increased with adulthood. Juveniles wasted considerable time in exploring resource clumps, and the smaller gape size associated with a small size was disadvantageous in handling food items such as dry grasses.

Continuous drought and livestock pressure reduced the grassland food abundance, supporting a generalised trophic niche use. Foraging theory suggested an optimal diet selection through successive addition of food items, ranked in terms of average food gain per unit handling time to maximise the net rate of food gain. Therefore, lower ranked foods would be deselected under higher food abundance, leading to specialisation (Pyke 1984). The results were in conformance with these predictions. During summer, there was a low density of dry grasses (*Chrysopogon, Cymbopogon*) and even lower densities of shrubs such as *Capparis decidua, Prosopis juliflora* and *Clerodendron*, of which only the latter was consumed. The monsoon brought forth a rich assemblage of herbs (*Borreria, Indigofera, Euphorbia, Anisomeles* and *Alternanthera*), succulent grass stocks and flowering shrubs (*Grewia, Vernonia* etc). Foraging was proportional to availability in the dry season but selective in the wet season, *Clerodendron* and insects were consumed only in summer, the latter for protein supplementation, a drought adaptation reported in committed herbivores (King 1996). An ontogenic, dietary shift from insectivory in juveniles to herbivory in adults, reported in this species by Minton (1966) was observed neither by Bhanotar and Bhatnagar (1977) nor in this study. Conducive environmental conditions were restricted to a short time span during which most of the lizards foraged avoiding spatial clumping. Such behavioural synchrony reduced conflicts and facilitated predator avoidance.

The field metabolic rate (Nagy 1982), estimated crudely from Nagy's relationship for iguanids (Nagy 1987), yielded a minimum required forage intake of 1.7 gm/day to maintain the energy balance. The observed feeding rate was more than twice this minimum requirement. Lizards compensated for the low food availability in the dry season with a surplus energy balance in the favourable season that would also be stored for hibernation. Similar trends were found in *Uromastyx aegyptius microlepis* (Robinson 1995). Moreover, the linear relation between the log-transformed body size and

mass suggested that lizards tended to grow rapidly to adult size and then accumulate mass.

In a typical *Uromastyx* habitat, the benefit from extensive foraging movements in a large territory in terms of a higher food encounter rate would be less than the costs of predation risk, energy expenditure in movements and territorial defence. This might have caused movement restrictions to an intensive area, site fidelity at least for a year and reduced territoriality in the periphery of the home range, primarily to conserve energy. The observed range size (0.2 ha ± SE =0.04) was 10-fold less than predicted (2.5 ha) by Turner *et al.* (1969). Male home ranges, however were much larger, a common feature in lizard ecology (Ferner 1974). The monsoon had reduced spatial use under the relative abundance of food, higher predation risks from Jackal, domestic dogs, Fox, raptors and cattle egrets, a smaller need of searching for mates and a greater need for conserving energy before entering the hibernation phase.

Resource dispersion caused the lizards to burrow in weak clumps. Hatchlings residing in maternal burrows during the initial 29 to 40 days of hatching, utilised a range of 6 to 12 m from their burrows, and were tolerated by adults (Bhanotar and Bhatnagar 1977). Burrows, generally located at the centre of core ranges, were also the centre of territoriality that started right after independent burrowing. Intraspecific competition for establishment of resource territories was high among juveniles. Juveniles were commonly found fighting for burrow acquisition that was followed by acquisition of territory. The extent of overlap between adjacent home ranges of two age-gender classes depended on their relative movements. Overlaps were minimal in the core, where a resident individual usually fought off an intruder. They were extensive in the fringes where confrontations were mostly mitigated through subtle aggressions. Such patterns were suggestive of territoriality in the core, but temporally determined resource sharing in the periphery of the home range. Previous studies reported hierarchy, territoriality (Stamps 1977; Heatwole and Taylor 1987) and mixed social interactions elicited by overcrowding (Hunsaker and Burrage 1969) that might have resulted here from spatial clumping of resources and burrowing substrate. Males showed relatively low aggression rates. Male-juvenile, male-female and male-male core range overlaps were similar during the study period. Thus, resource territoriality predominated over reproductive territoriality in this species. However, we had no observation of breeding as the study period included only a minor portion of the mating period. Hence, there is likelihood of resource based territories changing to breeding territories during the peak mating period. The core range of each male overlapped with one or two

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(sometimes exclusive) female ranges. The affinities of female(s) towards specific males caused high variability in inter-female range overlaps. This confirmed certain minimum reproductive chances for each male. But, entire ranges of some included even more females indicating that individuals differed in their reproductive strategies. Benefiting out of a high average longevity, some males probably postponed their surplus mating potential by minimising exploratory movements, to use the conserved energy later. Others possibly attempted opportunistic mating through energy-costly explorations. As the reproductive season coincided with the lean food availability period, such differences in mating strategies were of high evolutionary significance, and explained the wide variation in male range size.

Juxtaposing the livelihood strategy of this non-nomadic, generalised herbivore, avoiding predators through escape, against the nomadic, highly specialised insectivore *Moloch horridus* that freezes to avoid predators (Pianka *et al.* 1998) strikingly exemplifies the alternative evolution of correlated life history components.

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